Confederal Neural Organization in *Octopus vulgaris:*

Architecture, Photoreception, Sleep, and the Problem of Play

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Desde el rincón de la Izquierda

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Abstract

This paper examines four aspects of the cognitive biology of *Octopus vulgaris* which, considered together, point to a model of neural organization radically different from that of vertebrates: the peripheral distribution of most of its nervous system, the presence of functional photoreceptors in the skin, the existence of active sleep states analogous to mammalian REM, and the behaviors commonly described as 'play.' Regarding this last point, the paper proposes a conceptual dissolution: the label 'play' constitutes a

case of methodological anthropomorphism that can be resolved by appealing to the model of functional independence among the arms and to the absence of episodic memory in individual ganglia. The analysis of these phenomena through the confederal model additionally allows two further proposals: an objection to the claimed universality of Tononi's Integrated Information Theory, through the concept of Alt-phi — functional complexity achieved by organismic multiplicity as opposed to central organic integration —; and an explanation for the absence of culture in an intelligent animal, linked to the impossibility of centralized self-representation and, with it, of sociality.

1. Introduction

Octopus vulgaris represents, within the animal kingdom as a whole, one of the best-documented cases of intelligence that has arisen completely independently from that of vertebrates. Its last common ancestor with mammals was an organism of minimal neural complexity that inhabited the Cambrian seas approximately 530 million years ago (Kröger et al., 2011). From that bifurcation onward, the evolutionary line of coleoid cephalopods developed its own cognitive solutions, with no shared heritage from those that led to vertebrates. The result is an animal that Godfrey-Smith (2016) aptly describes as 'the closest thing to an alien intelligence we can find on Earth.'

The peculiarity of the octopus lies not solely in the size of its nervous system — some 500 million neurons, comparable to that of a dog (Young, 1963; Godfrey-Smith, 2017) — but in its architecture: approximately two thirds of those neurons are located

not in the central brain but distributed throughout the eight arms, in the form of peripheral ganglia (Hochner, Shomrat and Fiorito, 2006). This organization gives rise to a model that the present paper proposes to term ‘confederal,’ in contrast to the ‘centralist’ model that characterizes vertebrates, in which the cortex controls the periphery in a hierarchical, top-down manner.

The four phenomena analyzed below — neuronal distribution, cutaneous photoreception, active sleep, and play behavior — have received growing attention in the specialized literature but have rarely been examined in an integrated fashion. The aim of this paper is precisely that integration, with particular attention to the methodological problem posed by so-called ‘play’ in cephalopods.

2. Neural Architecture: The Confederal Model

The nervous system of *Octopus vulgaris* comprises approximately 500 million neurons distributed as follows: some 50 million in the central brain, between 130 and 150 million in the optic lobes — functionally differentiated from the executive brain — and around 300 million in the arm ganglia (Young, 1963; Godfrey-Smith, 2016). This distribution inverts the typical vertebrate proportion, where the vast majority of nervous tissue is concentrated in the central nervous system. In comparative terms, 50 million central neurons place the octopus in the range of the rat; the difference lies not in the central brain but in what surrounds it.

The basic processing unit is itself qualitatively distinct from that of the vertebrate. Octopus neurons are of the monopolar type, characteristic of invertebrates: a single extension emerges from the cell body and bifurcates in a T-shape, with one branch directed

toward the central neuropil where synapses occur and the other acting as an axon. The cell body, situated in the outer layer of the ganglion, is electrically passive and does not generate action potentials. In vertebrates, by contrast, the multipolar neuron has axons and dendrites emerging directly from the cell body, which is situated within the tissue and actively participates in processing. These are two distinct evolutionary solutions to the same problem of transmitting and processing information.

The octopus central brain is organized into more than 30 differentiated lobes, arranged in two masses literally traversed by the esophagus — an anatomical peculiarity without equivalent in vertebrates. Some lobes have recognizable functional analogies: the vertical lobe is the functional analogue of the mammalian hippocampus, involved in learning and visual memory; the peduncle lobe architecturally recalls the cerebellum; the higher motor centers are comparable to motor cortex, though without somatotopic organization — the octopus brain does not contain a body map like ours.

Each arm possesses an axial nerve cord with local ganglia that function as centers of sensorimotor integration for the suckers and adjacent musculature (Sivitilli, 2019). This organization allows the arms to execute complex behaviors without requiring real-time instructions from the central brain. The most direct demonstration of this autonomy is that an amputated arm continues to respond to stimuli and execute coordinated movements for an extended period after separation from the body (Sumbre et al., 2001).

The central brain operates, in this scheme, as a strategic authority: it determines high-level objectives — direction of movement, choice of prey — but does not micromanage execution. This organization has been described as ‘brain-down’ in vertebrates, as opposed to

what in the octopus might more precisely be termed, rather than the usual ‘arm-up,’ an ‘arm-arm’ dynamic: the arms do not send signals upward to the brain but instead act each within its own domain without consulting either the brain or the other arms. A recent investigation from the University of Chicago (Kuuspalu, Cody and Hale, 2022) has added a further element of complexity: the intramuscular nerve cords of the arms present lateral connections between arms situated on opposite sides of the animal, suggesting a layer of peripheral integration hitherto undocumented.

The political analogy proves heuristically useful: the octopus nervous system is not a decentralization — which implies a center that cedes competencies but retains them in the last instance — but rather a distribution of functional sovereignties. Each arm possesses genuine autonomy in its domain without the center being able to or needing to intervene in tactical execution. This is structurally different from the neural federalism that might be attributed to certain mammals with distributed motor cortex.

3. Cutaneous Photoreception: Seeing without Eyes

Octopus vulgaris is colorblind in the conventional sense: its retina possesses a single type of photoreceptor, which precludes wavelength discrimination by spectral comparison (Mäthger et al., 2006). Yet its capacity for chromatic camouflage is extraordinary, which for decades constituted a paradox without satisfactory resolution.

The solution arrived unexpectedly: Ramirez and Oakley (2015) demonstrated that the skin of *Octopus bimaculoides* contains

functional opsins — the same photoreceptor proteins present in the retina — and that isolated skin samples, with no connection to the brain or eyes, respond to light by expanding chromatophores. This phenomenon was termed LACE (Light-Activated Chromatophore Expansion). The response peaks with blue-green light, at a wavelength slightly different from that which activates the ocular opsin.

Maselli et al. (2025) have extended these findings to the optic lobes and suckers of the common octopus, confirming the presence of an extraocular photoreception system distributed across multiple tissues. The molecular signaling pathway identified in the skin is homologous to that of the eye, suggesting an evolutionary repurposing of the same photochemical mechanism in a peripheral context.

The most relevant implication for the confederal model is that camouflage can operate, at least in part, autonomously from the central brain. The skin sees and responds without any central processing. If the arm ganglia receive and process signals from cutaneous opsins — which anatomy makes plausible though it has not been precisely demonstrated — then each arm would constitute a rudimentary and independent visual system, capable of locally adjusting its pigmentation without consulting the executive brain.

This interpretation is consistent with the absence of a blind spot in the octopus. Unlike the vertebrate eye, where the optic nerve traverses the retina creating a zone devoid of photoreceptors, the octopus eye is constructed ‘in reverse’: the nerve inserts from behind the retina, leaving the receptor surface completely free (Ogura, Ikeo and Gojobori, 2004). The two visual systems — ocular and cutaneous — appear to serve distinct and complementary functions for the organism as a whole: high-resolution vision for

hunting and navigation in the first, local and automatic camouflage adjustment in the second.

The octopus eye constitutes, in itself, one of the most cited examples of convergent evolution. Vertebrates and cephalopods independently developed the camera-type eye — with iris, lens, vitreous humor and retina — from a common ancestor that possessed at most a simple photosensitive patch (Ogura et al., 2004). The common ancestor of both lineages lived more than 500 million years ago. This structural convergence reaches even the molecular level: 69.3% of genes expressed in the human eye have homologs — inherited from the common ancestral forebear — expressed in the octopus eye (Ogura et al., 2004), suggesting that the camera-type eye constitutes an almost inevitable solution to certain selective pressures.

4. Active Sleep and REM-Analogous States

For decades it was assumed that differentiated sleep states — particularly REM sleep, characterized by rapid eye movements and high-frequency brain activity — were exclusive to mammals and birds. Subsequent research extended this pattern to some reptiles and to the cuttlefish (*Sepia officinalis*), a cephalopod closely related to the octopus.

In 2021, a team from the Federal University of Rio Grande do Norte (Medeiros and Ribeiro, 2021) documented in *Octopus insularis* the alternation of two differentiated sleep states: a quiet sleep, characterized by immobility and muted coloration, and an active sleep of between 40 and 60 seconds duration in which the animal’s skin exhibits rapid and intense chromatic changes, the suckers

contract, the musculature stirs, and the eyes perform rapid movements. The animals showed elevated response thresholds to external stimuli during both phases, confirming that they were asleep and not merely in alert rest.

Pophale, Shimizu, Mano et al. (2023), from the Okinawa Institute of Science and Technology, confirmed these findings through high-density electrophysiological recording in the brain of *Octopus laqueus*, finding that electrical activity during active sleep was analogous to that recorded during wakefulness — a pattern characteristic of mammalian REM (Medeiros and Ribeiro, 2021; Pophale et al., 2023).

The chromatic changes of active sleep are especially notable because, unlike those of camouflage during wakefulness, they bear no relation to the animal's immediate environment. They occur in complete darkness or with the animal on monochromatic surfaces. The most widespread hypothesis is that they reflect spontaneous activity of the optic lobes — analogous to the mnemonic processing of mammalian REM — but the precise mechanisms remain undetermined (Mather, 2019). It should be noted, however, that this explanation does not consider the possible independence of color change due to the chromatic autonomy of the arms documented during wakefulness by Ramirez and Oakley (2015): it has not been established that the chromatic changes of active sleep necessarily originate from the central brain.

Memory consolidation and processing of information acquired during wakefulness are the most plausible functional hypotheses, though as yet undemonstrated in the octopus, for REM-analogous sleep (Medeiros and Ribeiro, 2021; Pophale et al., 2023). The existence of this active sleep in cephalopods has evolutionary implications of the first order. If it appeared independently in

vertebrates and cephalopods — lineages separated 530 million years ago — its function must be sufficiently advantageous to have been selected in two radically different neurological contexts, or it might even constitute a necessary condition beyond a certain cognitive complexity, for the reorganization of the processing system and the consolidation of memory.

5. The Problem of Play: Anthropomorphism and Conceptual Dissolution

The behavior described as ‘play’ in octopods constitutes one of the most illustrative cases of the methodological difficulties faced by comparative animal cognition. Its analysis requires distinguishing between the observed phenomenon — which is real and indisputable — and the category used to describe it, which may be inadequate.

5.1. The Observed Phenomenon

Studies on play in octopuses are based on two experiments of very different nature and structure, which the specialized literature has treated interchangeably under the same label. Their separate analysis is indispensable.

The first is that of Mather and Anderson (1999), conducted with *Octopus dofleini*: the animal directed jets of water through its siphon toward a pill bottle floating on the tank surface. The bottle could drift away and return due to the aquarium’s return current or remain more or less in equilibrium. The jetting behavior was repeated up to twenty times, with no food stimulus involved. The authors classified this behavior as an action ‘out of context’ and

termed it ‘exploratory play.’

However, examination of the experiment reveals that this classification is untenable. The water jet has a well-documented primary function: to drive unwanted objects away from the octopus’s proximity. That is precisely what the animal does in all cases documented by Mather and Anderson. That the object returns due to the artificial current — flowing back and forth within the tank given its closed parallelepiped geometry — an effect of the laboratory environment’s artifact, not an action of the octopus — and that the animal then repeats the jet does not constitute an out-of-context behavior: it is the same functional behavior reiterated in response to an object that persists in proximity. The attribution of intention that appears in the level 4 description of the appendix — ‘the octopus directs the jet, changing the object’s trajectory so that it approaches’ — is not supported by the data and confuses the physical result (the recursive approach of the object) produced by tank conditions with a deliberate action by the animal. In sum, Mather and Anderson’s experiment does not document play: it documents the functional and contextually appropriate use of the water jet in an artificial environment that produces effects unforeseen by the observer.

The second experiment is that of Kuba et al. (2006), conducted with *Octopus vulgaris* and Lego pieces. Fourteen specimens were exposed to the objects over seven consecutive days. Nine of the fourteen displayed behaviors that included holding the object with their arms, towing it through the tank, pushing and pulling it, and — most significantly — passing it from arm to arm. No significant differences were found as a function of food deprivation level, age, or sex. Kuba et al. (2003) had previously documented similar behaviors with other objects. This experiment is qualitatively distinct from the former: the observed behavior involves the arms,

not the siphon, and its nature is compatible with autonomous tactile and chemoreceptive exploration by the ganglia.

Burghardt (2015) and Pisula (cited in Mather, 2019) note that play, as defined in ethology, requires the behavior to be voluntary, pleasurable, apparently without immediate purpose, and to share structural elements with functional behaviors. The authors conclude that octopuses meet these criteria. This conclusion, as will be argued below, introduces unverified assumptions.

5.2. The Problem of Anthropomorphism

The category ‘play’ originates from the study of mammals and birds, in which it is associated with emotional states (pleasure, curiosity), social learning, and cognitive development. Applying it to cephalopods implies assuming, implicitly, that the observed behavior shares with mammalian play not only its external form but its motivational and functional bases.

Wynne (2007) argued that the study of animal cognition will advance only when it frees itself from anthropomorphic categories that precede experimental methodology. Bekoff (2000), by contrast, defended a ‘calibrated anthropomorphism’ as a heuristic tool: attributing mental states to the animal can facilitate the design of testable hypotheses, provided the attributions are treated as hypotheses and not as facts. The boundary between the two positions is clear: anthropomorphism as a starting hypothesis is methodologically legitimate; anthropomorphism as a conclusion disguised as empirical description — as occurs in the level 4 appendix of Mather and Anderson (1999) — is not.

The debate reflects a genuine methodological tension: the label ‘play’ can simultaneously be a useful tool for identifying a phenomenon of interest and an obstacle to its understanding,

insofar as it preselects the explanation.

5.3. A Proposal for Dissolution

This paper proposes that the debate over whether octopuses 'play' can be resolved by dissolving the question rather than answering it. The strategy is as follows: instead of asking 'Is this play?,' ask 'What is this behavior for?' and, from there, determine whether the category 'play' adds any explanatory power.

The case of Mather and Anderson (1999) falls outside this discussion for prior reasons: the description of the observed behavior is contaminated from the outset by a search bias that confuses the functional use of the jet — appropriate and in context — with an intentionality attributed to the unforeseen results produced by the laboratory's artificial environment. There is no phenomenon to dissolve because there is no phenomenon correctly described.

The case of Kuba et al. (2006) does require analysis. The observed behavior consists of repeated interaction with an object without immediate feeding consequences. If analyzed from the confederal model described in section 2, an alternative interpretation emerges that does not require appealing to higher-order mental states.

The suckers of each arm of *Octopus vulgaris* are multifunctional sensory organs: they simultaneously detect touch, pressure, temperature, chemical composition, and possibly luminosity (Ramirez and Oakley, 2015). Exploring a new object through the suckers provides the arm's local ganglion with information about the object's physical and chemical properties: texture, hardness, composition, buoyancy. This exploration has direct adaptive value, as it allows the classification of potentially edible or dangerous objects.

Within this framework, the behavior that researchers describe as ‘play’ can be interpreted as autonomous tactile and chemoreceptive exploration by one or several ganglia, without inter-arm coordination or central brain instruction. The observation that the octopus ‘pushes away’ the object and ‘retrieves’ it may simply reflect that one arm releases the object after having explored it, the object drifts away in the current, and a second arm — which possesses no information about what occurred, given the functional independence of the ganglia — picks it up as if it were new. The behavior of passing the object from arm to arm, documented by Kuba et al. (2006), is the most direct expression of this dynamic.

This interpretation has several advantages: it is consistent with the confederal model documented in neuroanatomy; it does not require attributing motivational states that are difficult to operationalize; it explains the individual variability observed by Kuba et al. (2006) in terms of differences in the exploratory activity of specific ganglia; and it is falsifiable through simultaneous recording of activity in ganglia of different arms during the behavior.

This interpretation also covers the intra-arm behavior documented by Kuba et al. (2006). The arm ganglion lacks episodic memory: it has no record of previous explorations nor awareness of the past, however immediate. It lives in perpetual present. Each contact with the object is, for the ganglion, functionally the first, since it cannot know that it has already explored it. Holding, releasing, and picking up the same object again does not constitute ludic reiteration but rather the only possible mode of operation for a system without history: exploring always as if for the first time, because for the ganglion it always is. Attributing ‘play’ to intra-arm behavior requires assuming that the ganglion possesses memory of the previous contact and decides, nonetheless, to repeat it without purpose. That assumption has not been demonstrated nor is it

necessary to explain the observed phenomenon.

What the researchers observe as an animal that 'plays' could in reality be nine partially autonomous sensory systems doing what they do when they have free time: exploring. The label 'play' does not describe the behavior of a unified animal, but rather the appearance that behavior has when observed from outside with categories designed for animals of centralized organization.

This does not imply that octopuses cannot 'play' in any sense of the term. It implies that the current label has not demonstrated any added explanatory power over the alternative functional description, and that its use introduces assumptions about central coordination and motivational states that have not been verified for cephalopods.

6. The Evolutionary Paradox: Intelligence without Inheritance

The four phenomena analyzed share an evolutionary background that makes their existence all the more remarkable. The lineage that led to modern octopods diverged from the nautiloids — cephalopods with external shells — approximately 416 million years ago. The internalization and subsequent loss of the shell in coleoids is an evolutionary event without direct precedent in the phylum Mollusca.

There is an unresolved debate regarding the adaptive sequence involved. Amodio et al. (2019) propose that it was the loss of the shell that drove the development of intelligence, by exposing these animals to unprecedented predatory pressures and forcing them to

colonize niches that required more complex behavioral strategies. Mollo, Amodeo and Ghiselin (2019) challenge this sequence, arguing that a minimal intelligence must have preceded shell loss, since the animals would otherwise have been incapable of surviving without protection. Amodio et al. (2019) respond that the hypothesis does not require an abrupt leap, but rather a gradual coevolution.

Whatever the sequence, the result is an animal that developed complex intelligence, including learning, memory, and the behaviors described in this paper, without transmitted culture, without social learning, without prolonged infancy, and with a lifespan of one to two years. Each generation reinvents its capacities from scratch, inheriting from previous generations nothing beyond what the genome can encode.

From a cognitive perspective, this suggests that what is commonly called ‘culture’ can be dissolved into the more general category of ‘learning.’ The octopus possesses individual learning; what it lacks is the externalization and transmission of that learning. The absence of culture is not the absence of intelligence: it is intelligence without collective memory.

But the absence of culture in the octopus is not merely a consequence of its lifespan or its semelparous reproduction. It is a consequence of its solitude. Culture requires a social animal: Whiten et al. (1999) documented 39 culturally transmitted behavioral patterns in seven chimpanzee populations, demonstrating that what defines culture is not the mere existence of learning but its social transmission between individuals. Without sociality there is no transmission, and without transmission there is no shared learning.

The octopus is a solitary animal, and this solitude is not accidental

with respect to its neural architecture. Sociality demands the capacity to represent the other as an equal — as another self, as a member of a 'we.' This projection requires, in turn, a prior self-representation: to attribute selfhood to the other, one must first possess a centralized self from which to project. A confederal system, with autonomous ganglia and without sufficient central integration to generate a unified self-representation, lacks the platform from which to construct that projection. The octopus can individualize other organisms — the literature documents that it distinguishes individual human caretakers and behaves differently toward each — but individualization is not recognition of subjectivity: it is recognition of differentiated objects in the environment, not subjects.

The sequence is therefore as follows: without a centralized self there is no self-representation; without self-representation there is no projection of selfhood onto the other; without that projection the category 'other like me' does not exist; without it there is no 'we'; without 'we' there is no sociality; and without sociality there is no culture. The absence of culture in the octopus is not a contingent deficit but a structural consequence of its confederal organization. A system that reinvents the wheel with every generation, but that is perfectly capable of doing so.

7. Conclusions

The joint examination of the four phenomena analyzed allows the following conclusions to be formulated:

First. The nervous system of *Octopus* constitutes a model of decentralized organization qualitatively distinct from that of vertebrates. It is not a variant of the same model but an evolutionarily independent solution to the problem of coordinating a

complex body. The denomination used here, ‘confederal’ as opposed to ‘centralist,’ captures this difference with greater precision than terms such as ‘distributed’ or ‘decentralized,’ which imply a cession of power from a center.

Second. The cutaneous photoreception documented by Ramirez and Oakley (2015) and extended by Maselli et al. (2025) is consistent with the confederal model: the skin responds autonomously to light, without central processing, locally adjusting pigmentation. The octopus’s camouflage does not require, in all its aspects, the mediation of the brain.

Third. The active sleep states documented in Medeiros and Ribeiro (2021) and confirmed in Pophale et al. (2023) constitute a case of functional — not homologous — convergence with mammalian REM, suggesting that the functions associated with this state (memory consolidation, information processing) represent adaptive advantages of sufficient magnitude, or even a necessary condition beyond a certain cognitive complexity, to be independently selected in two lineages without a recent common ancestor.

Fourth. The behaviors described as ‘play’ in octopods are real as observational phenomena but require differentiated analysis. Mather and Anderson’s (1999) experiment does not document play but rather the functional and contextualized use of the siphon in an artificial environment whose geometry produces effects not attributable to the animal (much less desired by it). Kuba et al.’s (2006) experiment does describe a relevant phenomenon, interpretable as autonomous tactile exploration by individual ganglia without the need to appeal to higher-order or central cognition. This interpretation is economical in its assumptions, consistent with known neuroanatomy, and falsifiable through simultaneous electrophysiological recording of multiple arms.

Fifth. The case of the octopus allows an objection to be formulated against the claimed universality of Tononi's Integrated Information Theory (2004; 2008). Tononi constructs phi upon an implicitly chordate-centric model: the integration his measure quantifies is integration within a central organ that concentrates processing. Presented as a universal measure, phi assumes without justification that central integration is the sole pathway to functional complexity. The octopus constitutes a counterexample: its functional complexity is high — it solves problems, adapts to changing environments, executes sophisticated hunting and evasion strategies — while its central integration is low, with autonomous ganglia and an executive brain of 50 million neurons. What is here proposed as Alt-phi describes the alternative pathway: functional complexity achieved not through organic integration — within an organ — but through organismic multiplicity — within an organism composed of autonomous units. The pathway is not the complexity of the organ but the complexity of the organism. The data presented in this paper make plausible the hypothesis that functionality and central integration are dissociable: the former does not necessarily require the latter.

Sixth. The evolutionary paradox of an animal of high intelligence without transmitted culture is dissolved upon recognizing that culture requires sociality (Whiten et al., 1999), and that sociality requires a centralized self-representation that the octopus's confederal architecture cannot generate. To represent the other as an equal — as another self — it is necessary first to possess a unified self from which to project. A confederal system lacks that platform. The octopus individualizes objects in its environment, including other organisms, but does not construct the category 'other like me,' nor, therefore, a 'we.' Without 'we' there is no sociality; without sociality there is no transmission of learning;

without transmission there is no culture. What the octopus lacks is not intelligence or learning, but the mechanism — social, and ultimately neural — necessary to externalize and transmit what each individual learns. The species does not accumulate: it reinvents the wheel with every generation, but is perfectly capable of doing so.

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Tuesday, April 14, 2026

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